MISSISSIPPIAN DISCINID BRACHIOPODS ATTACHED TO A SOFT-BODIED ORGANISM[1]

R. PETER RICHARDS

Department of Geology, Oberlin College, Oberlin, Ohio 44074

ABSTRACT

A concretion from the lower Mississippian Meadville Shale Member of the Cuyahoga Formation near Lodi, Ohio, preserves a population of *Orbiculoidea newberryi* Hall in life position, associated with what is interpreted to be an unidentified soft-bodied organism. The brachipods show a diffuse unimodal orientation, parallel to the axis of the "host" organism, in what was probably an upward direction during the life of the group. Recruitment to the assemblage apparently was periodic. Two size classes, perhaps representing yearly recruitment, contain about equal number of individuals. Most individuals were attached to the soft-bodied organism, but six of the nine smaller specimens were attached to adults of the species. The assemblage is similar to recent discinid assemblages from quiet water and suggests a continuity of basic life style throughout a major part of the fossil record.

INTRODUCTION

Assemblages in which brachiopods are preserved in their life orientations are of great value to the study of brachiopod paleoecology, because they provide direct access to information about life habits which often cannot be obtained with certainty in any other way. Most Paleozoic brachiopods, especially among the Articulata, belong to extinct orders, and comparisons with modern analogs are therefore possible only at a very general level. In other cases, such as the one described here, rather close modern relatives exist and have been studied, permitting fruitful comparison.

This paper describes a life assemblage of *Orbiculoidea newberryi* Hall found in a concretion coming from the Mississippian Cuyahoga Formation, Meadville Shale Member, and compares it with assemblages of other Discinacea from the Ordovician (Richard, 1972) and the Recent (Paine, 1962; Davidson, 1888). The specimen is in the Oberlin College Paleontology Museum, catalog number OC 8359.

LOCALITY AND STRATIGRAPHIC SETTING

The concretion described in this paper was collected from talus at the base of a stream-cut cliff on the south bank of the West Fork of the Black River, 4.5 miles west of the center of Lodi, Ohio, along U.S. 224 (2 112 000 feet East, 494 900 feet North, Lodi, Ohio 7 ½ min. quadrangle). The level from which the concretion came cannot be established with confidence, for several horizons in the outcrop have numerous concretions. However, the entire outcrop is in the lower Meadville Shale Member of the Cuyahoga Formation.

The Meadville Shale as seen here is a variable unit composed mostly of dark shales, but with siltstones, limestones, and laminated and massive sandstone with planar and cross bedding. Individual beds are generally of short lateral extent. Contacts are gradational in places and sharp in others. All lithologies may be fossiliferous. Limestones are widely spaced and are composed primarily of echinoderm, ectoproct, and brachiopod fragments. Fragments of land plants are common in the shales (Kesling and Le Vasseur, 1971, p. 308), and larger plant fossils, including branches of lycopsids, are occasionally found in the limestones. Ironstone nodules are common at certain horizons in the shales, and ironstone zones occur in the limestones.

Most sandstone and siltstone beds are lenses elongated in one direction. These lenses typically have sharp contacts with the underlying shales, and their basal surfaces contain tool marks which are oriented parallel to the length of the

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lens. The sandstones are graded, commonly with a layer rich in fossil hash at the base. This graded layer is overlain by a sequence of massive sandstone, laminated sandstone, and in places, siltstone. The contact of a sandstone with the overlying shale is typically gradational. Bedding planes within some lenses preserve current ripples, which indicate a direction of transport parallel to the sole markings.

This sequence of lithologies is interpreted as having been formed in a shallow marine environment not far from land, but below wave base, and characterized by slow deposition of clay-sized sediments. Occasional agitation of shallower water in regions nearer to shore produced turbidity flows which deposited coarser materials (sandstone to siltstone, with shell fragments) in elongate lenses. The environment is viewed as a quiet-water one, probably with a rather soft mud bottom and with a generally low rate of sedimentation, but subject to infrequent localized rapid deposition of coarser sediments.

This interpretation agrees in its general aspects with those given by Kesling and Le Vasseur (1971, p. 308–314) and by Osgood and Szmuc (1972, p. 10) for other outcrops of the Meadville Shale in northeastern Ohio. It is intended as a model only for the locality described above, however, and does not suffice to explain the entire local Meadville section, the upper beds of which appear to have formed in a shallower water environment, comparable to the one from which the turbidites of the lower section were derived.

THE FOSSIL ASSEMBLAGE

The fossil assemblage is preserved in a subround ironstone concretion about 7 cm in diameter. Both halves of the concretion were recovered, and are shown in figure 1. The surface along which the concretion broke bears a series of low concentric ridges over most of its area. In addition, a series of finer, branching ridges occurs near the edge of the concretion, near the point about which the concentric ridges are centered. No skeletal material, stain, or microskeletal elements could be found on this surface. However, the regularity of the concentric arcs, together with details discussed below of the relationship of the brachiopods to the surface, strongly suggests that this surface is the trace of a soft-bodied organism. It seems likely that the soft-bodied organism was an animal, if only because a plant rapidly entombed in a concretion would be likely to leave a carbon trace. The animal in question cannot be placed with certainty even in a phylum, but the radial symmetry implied by the concentric arcs is suggestive of either the Porifera or the Cnidaria.

The brachiopods (*Orbiculoidea newberryi*) are concentrated on or near the impression of the soft-bodied organism. The majority are oriented with their pedicle valves adjacent to the soft-bodied organism and parallel to it. The six exceptions are all small individuals, less than 3 mm long, which are attached to larger brachiopods. Five of these are attached to the underside of the same pedicle valve. The lengths of those brachiopods complete enough to measure, and the orientations of their anterior-posterior axes are recorded in table 1. Their positions on the organism are indicated in figure 2, which also shows the way their orientations were measured.

The orientations of the brachiopods appear to have some modality: nine of the measurements fall between 180° and 300°. However, this modality is not significant even at the 0.2 level, as determined by the Komolgorov-Smirnoff test (see Tanner, 1955, for a discussion of the application of the Komolgorov-Smirnoff test to orientation data). The orientation of each brachiopod was compared also with the orientation of a radius drawn through the apex of the brachiopod from the center of the concentric arcs of the soft-bodied organism (fig. 3). The angle between these two orientations is strongly modal: all values fall between 0° and 90°:

Specimen number:	1	2	3	4	5	6	7	11	13	15	17	19
Angular deviation:	16°	39°	9°	43°	55°	20°	2°	88°	68°	86°	16°	74°

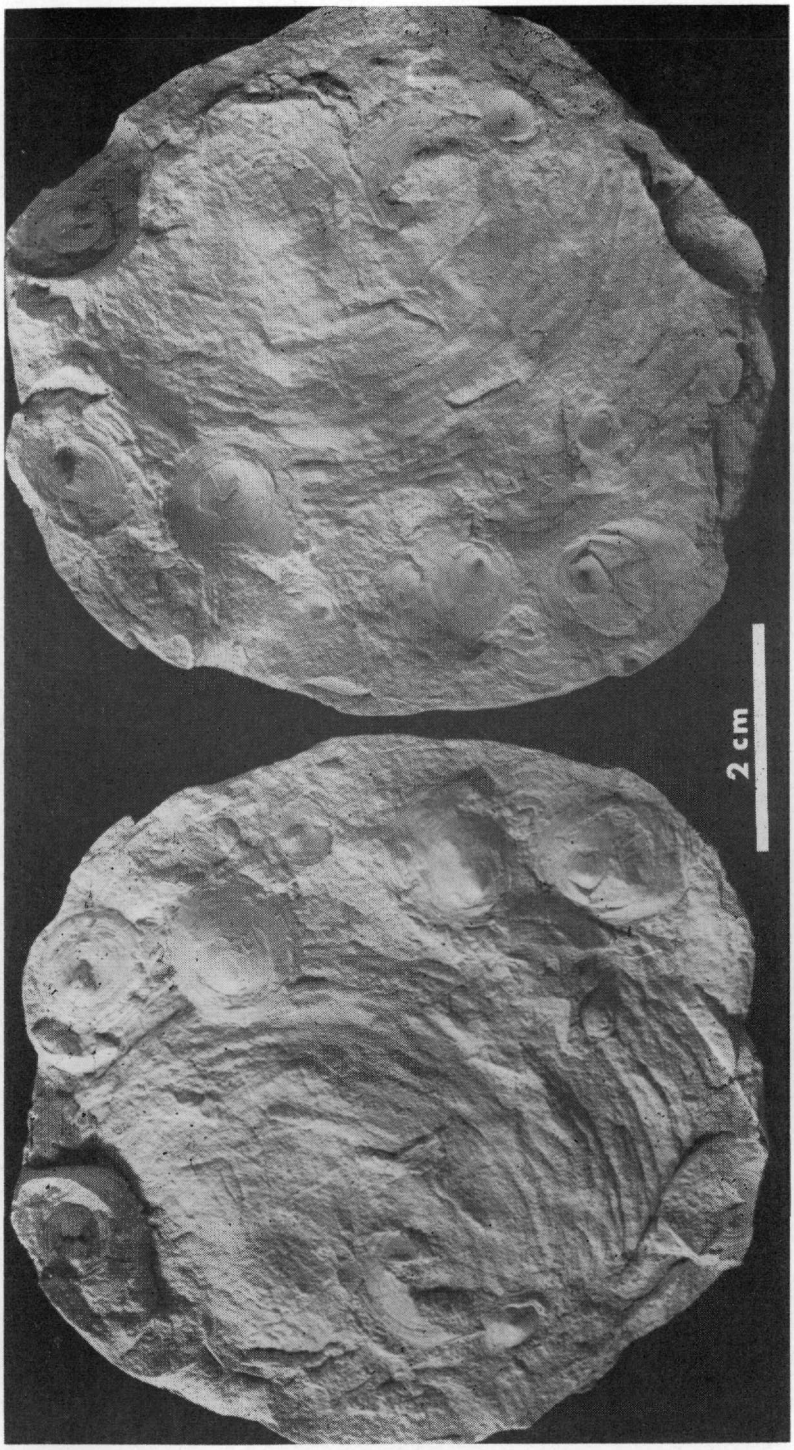
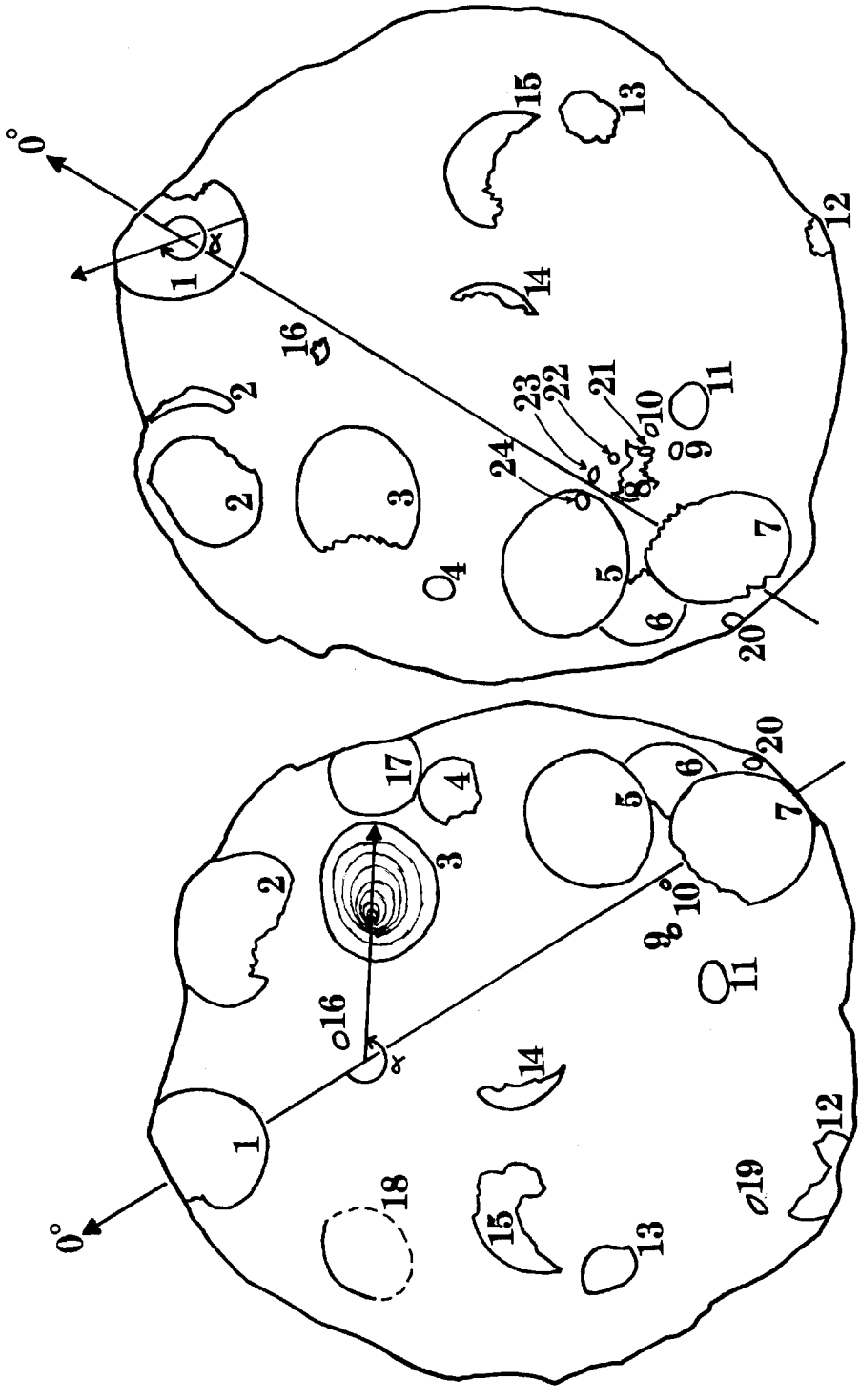


FIGURE 1. The Mississippian discinid *Orbiculoidea newberryi* in life position attached to an unidentified soft-bodied organism, preserved in an ironstone concretion. The two halves of the concretion are shown. Some individuals are visible on only one surface. Scale is 2 cm.


0°
1
16
2
2
3
4
5
6
7
20
24
23
22
21
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11
9
8
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14
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0°
1
2
3
17
4
16
18
15
13
14
5
6
20
7
10°
9
11
19
12

FIGURE 2

TABLE 1

Orientation, shell length, and association of 24 individuals of Orbiculoidea newberryi[1]

Individual	Orientation (°)	Shell length (mm)	Attached to
1	253	14.6	Soft-bodied organism
2	225	10.9	Soft-bodied organism
3	236	12.0	Soft-bodied organism
4	187	7.1	Soft-bodied organism
5	264	14.1	Soft-bodied organism
6	189	>8	Soft-bodied organism
7	202	13.8	Soft-bodied organism
8	—	>8	Soft-bodied organism
9	—	1.6	Brachiopod 8, pedicle valve
10	—	1.1	Brachiopod 8, pedicle valve
11	276	4.0	Soft-bodied organism
12	—	>8	Soft-bodied organism
13	77	~8	Soft-bodied organism
14	—	>8	Soft-bodied organism
15	85	12.8	Soft-bodied organism
16	—	<8	Soft-bodied organism
17	256	~9.5	Soft-bodied organism
18	—	>8	Soft-bodied organism
19	103	2.8	Brachiopod 12, brachial valve
20	—	2.4	Soft-bodied organism
21	—	1.6	Brachiopod 8, pedicle valve
22	—	1.1	Brachiopod 8, pedicle valve
23	—	1.3	Brachiopod 8, pedicle valve
24	—	1.1	Soft-bodied organism, under brachiopod 5

[1]Orientation measurements are the angles in degrees of the anteriors from an arbitrary reference line (see fig. 2). Estimated lengths of the shells of incomplete or incompletely exposed specimens are preceded by ~; individuals too fragmentary to allow an estimate of length are classed as "big" (greater than 8 mm) or "little" (less than 8 mm) on the basis of the radius of curvature of the part of the shell which is present.

This statistic is significantly different from a random distribution, even at the 0.01 level.

The exact significance of this last result is unclear, because of uncertainty about the identity and form of the "host" organism. The interpretation favored in this paper is that the soft-bodied host was of roughly conical shape, and probably lived with the apex down, in the manner of Recent basket sponges. The form of the fossil soft-bodied organism indicates a cone with an apical angle of about 80°. During burial, the organism collapsed, forming two superimposed planar sheets which were sectants of circles (see fig. 4). Brachiopods growing on the outer surface of this conical organism would probably have oriented themselves with their anterior margin upward along the cone, in order to maximize feeding efficiency in a quiet environment, where food settled down from above. Upon

EXPLANATION OF FIGURE 2

FIGURE 2. Line tracing of figure 1, showing the position of the brachiopods and the reference line relative to which they were measured to produce the data in table 1. Note that the angles are measured clockwise on the right half of the concretion and counterclockwise on the left half.

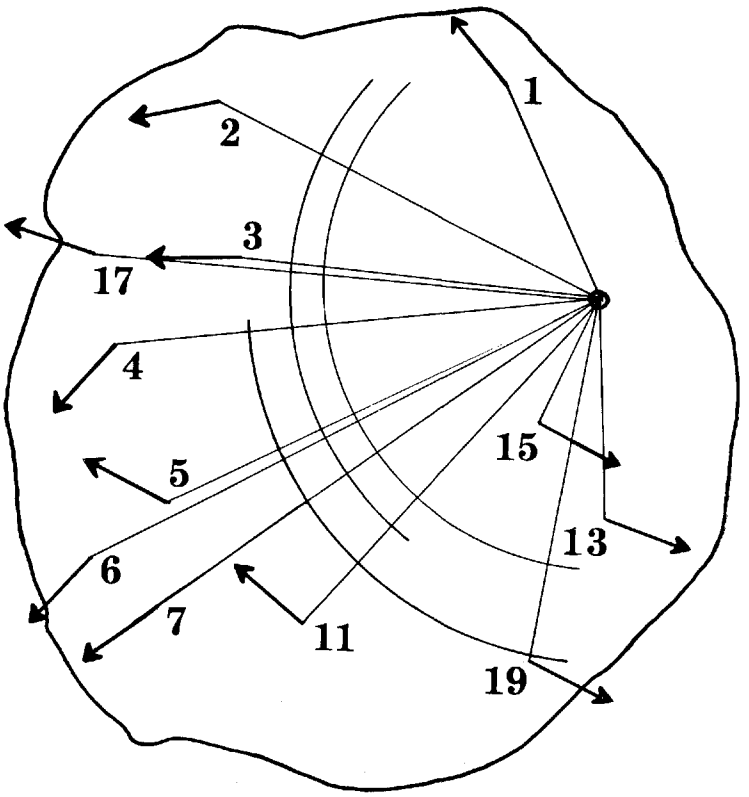

FIGURE 3. Line tracing of right-hand half of the concretion, to show how the measurements on page 178 were derived. The arrows mark the orientations of the anterior-posterior axes of the brachiopods; the arrow heads indicate the anterior ends of the axes. The light lines are radii of the soft-bodied organism, all directions which would have been up if the organism was of conical shape and was oriented with apex downward.

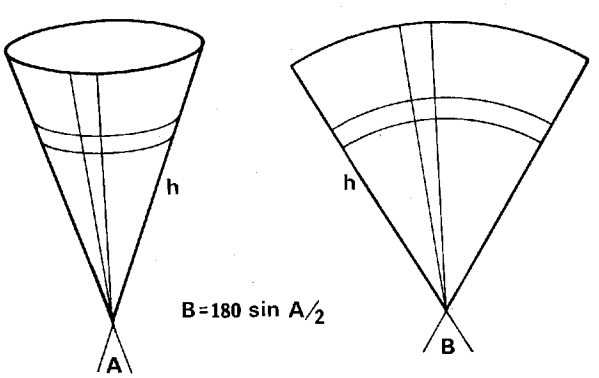

FIGURE 4. The flattening of a conical organism to form two sectants of a circle. The slant height of the cone (h) is the radius of the circle of which the sectant is a part. The angle of the sectant, B, can be shown to be equal to 180° sin A/2. Note the transformation of "growth lines" to concentric arcs and of various "upward" orientations to radii of the sectant.

collapse of the host, these orientations would lie along radii of the sectant, and the anterior-posterior axis of a brachiopod would coincide with the radius of the sectant drawn through the beak of the brachiopod. This model for the form of the host explains the orientations of the brachiopods, and their occurance above and below the plane of the concretion, always with their pedicle valves closest to their host.

Because the brachiopod population was entombed in the concretion with the individual shells articulated and in apparent life position, the brachiopods probably all died at the same time. The size-frequency distribution for the population (fig. 5) suggests two (seasonal?) peaks of larval recruitment with reduced

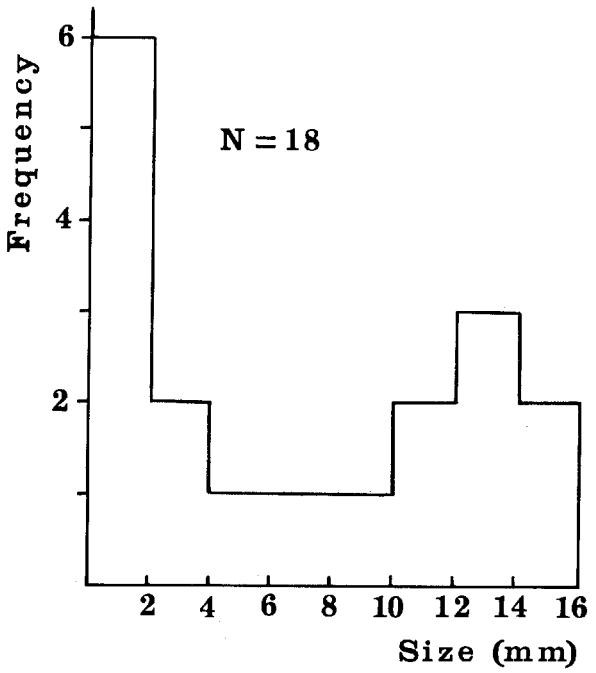

FIGURE 5. Size-frequency distribution for the 18 specimens of *Orbiculoidea newberryi* complete enough to measure. Size was measured with vernier calipers along the anterior-posterior axis, located by the orientation of the pedicle slit on pedicle valves and by the eccentric position of the apex of brachial valves.

recruitment between. The younger individuals in the population show settling behavior different from the older ones, which are attached to the "host," for, of the eight brachiopods less than 3 mm long, six are attached to older brachiopods. Five of these and one of the remaining two are attached in protected positions between older brachiopods and the soft-bodied organism (table 1).

COMPARISON WITH OTHER DISCINACEA

In an earlier paper (Richards, 1972), I described aspects of the ecology of the Ordovician discinid *Trematis millepunctata*. The ecology of this earlier discinid appears quite different from that of *Orbiculoidea newberryi*. *Orbiculoidea newberryi* shows gregarious behavior, which involved attachment of spat to adults. *Trematis millepunctata* was apparently gregarious only to a moderate extent. Individuals in assemblages discovered to date are of roughly equal size, and spat and juveniles have not been observed together in these assemblages. Choice of both protected and exposed microhabitats is involved in this *O. newberryi* assemblage, whereas only protected habitats seem to have been selected by populations

of *T. millepunctata* living in agitated waters and only exposed habitats by populations in quieter water.

The Recent species of *Discinisca*, described by Paine (1962) and Davidson (1888), show a range of ecological behavior which encompasses that of both *Trematis millepunctata* and *Orbiculoidea newberryi*. *Trematis millepunctata* is quite comparable to *Discinisca strigata*. Intertidal populations of *D. strigata* described by Paine are similar to shallow-water populations of *T. millepunctata* is showing preference for protected habitats and in not attaching to other individuals (Richards, 1972, p. 390). *Trematis millepunctata* which lived in relatively quiet water were apparently not gregarious, nor did they seek protected habitats. This pattern is analogous to the behavior of populations of *D. strigata* living in deeper water (Broderip, 1833).

In contrast, two Recent species of *Discinisca* typically form clusters. These species, *D. laevis* and *D. lamellosa*, live at depths of between 5 and 25 fathoms, attached to rocks, shells, wood, or other members of their species (Davidson, 1888, p. 196–198). By attaching to these substrates, individuals in different stages of growth form masses which live even in sandy environments. This pattern is similar to the gregarious behavior of *Orbiculoidea newberryi*, but involves more individuals packed more tightly in a typical cluster.

Paine (1962, p. 598) showed a unimodal size-frequency distribution for a population of intertidal *Discinisca strigata*, which he believed was indicative of a single prolonged annual recruitment period, with few or no individuals living as long as two years. The size-frequency distribution for *O. newberryi* shown in figure 5 could be interpreted in the same way, assuming that the assemblage was buried during the season of larval settling.

It must be remembered that these comparisons are based on one life assemblage each from the Ordovician (*Trematis millepunctata*) and the Mississippian (*Orbiculoidea newberryi*), on inferences from other specimens of *T. millepunctata* not actually found in life position, and on rather few detailed observations of modern discinids. If the indications of these few specimens are valid, however, they indicate that the Discinacea have been a conservative group ecologically. The basic ecology of recent species seems to have been established long before the end of the Paleozoic. If there is a pattern of change, it would seem to be toward more strongly gregarious behavior, which allows the exploitation, by recent species, of sandy substrates hostile to most other epifaunal brachiopods.

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